Life on the edge: do body size and drinking dependency influence how birds deal with the heat in South Africa's most extreme desert?

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Hot Birds RESEARCH PROJECT

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Abstract

Climate change-induced increases in air temperature pose a substantial risk to birds inhabiting arid environments. Terrestrial endotherms, such as birds, can respond to high temperatures by moving to cooler microsites, increasing heat dissipation behaviour and/or suppressing activity. Previous studies have suggested that larger bird species may have a greater suppression of activity (e.g. foraging) than smaller species at high air temperatures. However, this body mass effect may be confounded by drinking behaviour, since different species have diverse drinking ecologies. Using four species of lark that inhabit the Tankwa Karoo National Park, I investigated whether foraging activity and other heat-influenced behaviours were influenced by body mass or drinking behaviour when comparisons were constrained within a single family. These lark species were: Red-capped Lark (24 g), Spiked-heeled Lark (25 g), Karoo Lark (29 g) and Large-billed Lark (45 g). There was a two-fold difference in body mass between the lightest (Red-capped Lark) and the heaviest (Large-billed Lark). Moreover, two of these lark species drink surface water (drinking larks; Red-capped and Large-billed Lark) and two do not (non-drinking larks; Spike-heeled and Karoo Lark). I also collected data on other passerines present in the Tankwa Karoo for comparison to the larks. Black bulb thermometers were used to measure the thermal landscape and a combination of instantaneous scan samples and focal observations to record bird behaviour. Black bulb temperatures were as much as 8.16 °C cooler in shaded than in sunny locations. Similarly, black bulb temperatures were as much as 8.02 °C cooler off the ground than on the ground. The results from scan sample data showed limited support that foraging was negatively correlated (although non-significant) with mass between lark species as temperatures increased; however, data from focal observations suggested larks that obtain all water from food had a greater reduction in foraging as temperatures increase than larks that drink free surface water. Within scan samples, heat dissipation and shade-seeking behaviour appeared to be more strongly influenced by whether the species drinks free surface water or not than by differences in body mass. Furthermore, drinking larks dissipate heat at lower temperatures and seek shade at higher temperatures than non-drinking larks. Foraging intensity was higher in the sunny microsites as compared to shaded microsites for all species, suggesting that drinking larks might gain an energetic benefit due to increased heat tolerance. Therefore, non-drinking species may be vulnerable to foraging-thermoregulation trade-offs under

climate change. However, ongoing drying trends in the Tankwa Karoo and reduced availability of surface water may make drinking species more vulnerable to climate change in the future than non-drinking species.

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Plagiarism Declaration

I understand what plagiarism is and declare that all that this is all work of my own unless acknowledged.

Signed: Signed by candidate

Date: 09/02/2020

Introduction

Global climate change is recognised as one of the foremost and most extensive threats to biodiversity and one of the greatest current conservation challenges (Parmesan & Yohe 2003; Boyles et al. 2011; Dawson et al. 2011; McKechnie et al. 2012; Department of Environmental Affairs 2013). Anthropogenic activity is the main contributor to the increasing concentration of greenhouse gases in the Earth's atmosphere, which has subsequently been linked to climate warming (IPCC 2007; Solomon et al. 2009). One of the most prominent outcomes of climate change is that mean annual temperatures are elevated above that what can be explained by natural variation (IPCC 2007; Mora et al. 2013). In the last century, increased concentrations of carbon dioxide and other greenhouse gases in the atmosphere has caused a 1.0°C increase in Earth's mean temperature (IPCC 2018).

Climate change-induced temperature increases may pose novel thermoregulatory challenges for endotherms; especially those that are already living in hot and arid environments (McKechnie et al. 2012). Endotherms are animals, such as birds and mammals, that depend predominantly on evaporative cooling or metabolic heat production to maintain a constant body temperature (Bakken 1976). Endotherms living in such environments are exposed to air temperatures (T_{air}) that approach and often exceed their body temperature (Wolf & Walsberg 1996). Moreover, they often experience environmental temperatures considerably higher than the air temperature as a consequence of conduction, convection and especially radiation (Bakken 1976). Exposure to elevated temperatures can intensify the physiological costs of keeping cool (in terms of energy and water) and cause increases in body temperature (T_b), with prolonged exposure initiating heat stress and potentially resulting in lethal hyperthermia (Williams & Tieleman 2005; McKechnie & Wolf 2010; McKechnie et al. 2012). For example, periods of increased temperatures have resulted in several mass die-offs of mammals (e.g. bats and humans; Whitman et al. 1997; Welbergen et al. 2008) and birds (Saunders et al. 2011).

Birds may be particularly vulnerable to rising temperatures due to the general characteristics of having a small body size and being primarily diurnal (McKechnie & Wolf 2010). Birds can control and prevent their body temperature from reaching lethal limits through physiological

(e.g. facultative hyperthermia (increasing body temperature above normal during heat stress) and evaporative water loss; Boyles et al. 2011) and/or behavioural thermoregulation (e.g. seeking shade; Sears et al. 2011). Behavioural thermoregulation can be expressed in three ways: shade-seeking, activity suppression and posture adjustment (Wolf 2000; Porter & Kearney 2009). Birds can employ shade-seeking and use thermally-buffered microsites (e.g. shaded areas) to minimise physiological costs as temperatures increase (Kearney et al. 2009; Sears et al. 2011; Huey et al. 2012; Carroll et al. 2015; Cunningham et al. 2015). For example, Northern bobwhites *Colinus virginianus* were able to reduce their exposure to high temperatures by on average 10.4°C through seeking cooler microsites (Carroll et al. 2015). Thermally-buffered microsites could therefore prove to be vital refuges for birds in the context of climate change, as their use could result in a reduction in energetic costs, risk of dehydration and exposure to lethal temperatures (Kearney et al. 2009; Boyles et al. 2011; Sears et al. 2011; Huey et al. 2012; Scheffers et al. 2014; Carroll et al. 2015). As a result, several studies have emphasised the value of acquiring knowledge about how microsites can thermally buffer species from high temperatures and aid in their conservation (Hannah et al. 2014; Scheffers et al. 2014).

Behavioural thermoregulation and shade-seeking is not without costs and may inhibit other processes and activities from occurring (Wolf & Walsberg 1996). For example, behavioural thermoregulation can elicit trade-offs (such as, changes in time-activity budgets and reduced foraging success) which lead to sublethal fitness costs, such as reduced body condition, reproduction and long-term survival (Wolf & Walsberg 1996; Tieleman & Williams 2002; du Plessis et al. 2012; Cunningham et al. 2015; Edwards et al. 2015; Pattinson & Smit 2017; van de Ven et al. 2019). Small diurnal endotherms often are compelled to forage in the hottest microsites within the environment and as a result have high heat loads that need to be dissipated (Wolf & Walsberg 1996; Weathers 1997). Therefore, shuttling between cooler and warmer microsites may be an essential thermoregulatory strategy to cope with these heat loads. However, cooler microsites may offer inferior foraging opportunities, for example, Common Fiscals *Lanius collaris* incurred a 50% reduction in foraging success when moving away from perches in the sun to those in the shade (Cunningham et al. 2015). Southern Yellow-billed Hornbills *Tockus leucomelas* have a trade-off between thermoregulation (i.e. increased time in cooler microsites and panting) and foraging, with increased time in cooler

microsites reducing foraging efficiency and causing a subsequent decline in body condition (van de Ven et al. 2019). Thus, birds are confronted with the trade-off of suppressing activity and decreasing foraging effort in warmer microsites to reduce the risk of lethal hyperthermia, or maintaining the same level of effort in hot microsites, but increasing their risk of lethal hyperthermia and dehydration (Williams et al. 1999). With a warming climate, these trade-offs may become exacerbated (Mason et al. 2017).

Body size is a fundamental trait that influences the potential trade-offs birds make between thermoregulation and other behaviours, and ultimately their vulnerability to climate change (Weathers 1981; Porter & Kearney 2009; McKechnie et al. 2012). Larger birds may have more pronounced trade-offs between sustained levels of activity and thermoregulation than smaller birds at high air temperatures (Smit et al. 2016). This may be due to the fact that heat transfer between the bird and the environment is proportional to their surface area, while heat retention is proportional to body mass (Weathers 1981; Tieleman & Williams 1999; Williams & Tieleman 2001; McKechnie et al. 2012). Larger and smaller birds should have different responses to increasing temperature. For example, larger species may respond by utilising heat storage and facultative hyperthermia to maintain body temperature below lethal limits, as they have a greater capacity to store water and energy, slower metabolic rate and higher thermal inertia (heat in larger birds is dissipated more gradually as the surface-area to volume ratio decreases) compared to smaller species (Wolf & Walsberg 1996; Williams & Tieleman 2001; McKechnie & Wolf 2010; Zamora-Camacho et al. 2014). These factors in turn would allow larger species to endure longer periods of extreme heat than smaller birds (Wolf & Walsberg 1996; McKechnie & Wolf 2010). Small species, in contrast, have high metabolic rates (i.e. have to forage more often) and lower capacity to store water and other resources (Wolf et al. 1996; Simmons et al. 2004). They gain heat more rapidly from the environment and require proportionately more water for evaporative cooling as temperatures increase (Williams & Tieleman 2001; Martin et al. 2015). As a result, small species are expected to be less likely to survive during extreme heat events (Simmons et al. 2004; McKechnie et al. 2012). However, smaller body size may increase the efficacy of convective cooling and thus present thermoregulatory advantages so long as their environmental temperature remains lower than body temperature (Cunningham et al. 2013). Having a low thermal inertia may be beneficial for smaller birds, since they may be able to

offload heat faster than larger birds when moving into cooler microsites (Wolf & Walsberg 1996). Smaller birds may also benefit from the greater availability of microsites that are inaccessible to larger birds (Wolf & Walsberg 1996; Williams & Tieleman 2001; Huey et al. 2012). Therefore, with the contrasting evidence, it is difficult to predict the exact relationship between body size and patterns of behavioural thermoregulation.

Furthermore, the relationship between increasing temperatures, body mass and thermoregulatory behaviour might be may confounded by the influence of drinking dependency (Smit et al. 2016). Drinking dependency refers to whether a bird drinks surface water or not, as some bird species habitually drink from free water sources, whereas others gain all their water from diet and metabolism (Dawson 1982; Williams & Tieleman 2001; du Plessis et al. 2012). Drinking species are able to replace expended water more easily and as a result use water more freely in order to dissipate greater heat loads than non-drinking (Smit & Mckechnie 2015; Czenze et al. 2020). For example, drinking species in the Kalahari Desert exhibit a lower air temperature threshold at which they started displaying heat dissipation mechanisms compared to non-drinking species that use less water-costly thermoregulatory behaviours in order offload heat (Smit et al. 2016). This would suggest that non-drinking species may experience trade-offs between water conservation and heat dissipation (Dawson & Bartholomew 1968). Non-drinking species may have an elevated risk of dehydration with increased temperatures, since they are not capable of predictably replacing expended water (Smit & Mckechnie 2015). To avoid dehydration, these species may be forced to forage in hot conditions to obtain water, although foraging under these conditions may exacerbate their water loss as increased thermoregulatory water demands may be greater than their dietary water intake (Tieleman et al. 2003; du Plessis et al. 2012). These factors suggest that non-drinking species may be more vulnerable to climate change. However, the dependence of drinking species on surface water may increase their vulnerability to climate change as many regions are predicted to become more arid and this could consequently affect the availability of water sources (Serdeczny et al. 2017; Iknayan & Beissinger 2018). Therefore, it is vital to understand the extent to which drinking dependency influences these potential trade-offs.

Larks (Alaudidae) represent an ideal model system in which to test hypotheses regarding behavioural thermoregulation and trade-offs since these species are all ground-foraging, have

similar diets, behaviour and mutual phylogenetic history (Williams & Tieleman 2001). Moreover, within the Alaudidae family there is a diverse range of drinking behaviour from species that live completely independent of water (e.g. Red Larks *Calendulauda burra*; Dean & Ryan 2005a) to others that are obligate drinkers (e.g. Red-capped Larks *Calandrella cinerea*; Dean 2005b). The Alaudidae family consists of small to medium sized birds with substantial variation in mass ranging from 12 g to 75 g (de Juana et al. 2004). Furthermore, this family is prominent in hot and arid environments, with over 80% of the world's larks occurring in Africa (Willoughby 1971; de Juana et al. 2004), which has been identified as the most vulnerable continent to the impacts of climate change (IPCC 2014; Niang et al. 2014).

I studied the influence of body size and drinking dependency on behavioural thermoregulation in four species of larks (Order: Passeriformes, Family: Alaudidae) in the Tankwa Karoo National Park; which is one of the most extreme arid environments in South Africa. Climate change projections predict that the region will only become drier (Serdeczny et al. 2017). Moreover, I included other passerine species found in the Tankwa Karoo in this study for comparison with the larks. I hypothesise that the ability of birds to remain active as air temperatures increase is correlated with body mass because heat dissipation is influenced by the surface area to volume ratio and thermal inertia, which control heat flows from the bird's body to the environment and vice versa. Larger birds should gain heat from the environment slower than smaller birds, but also lose the heat slower. Therefore, I predicted that smaller birds will be more active and forage more at higher temperatures than larger birds as they are able to dissipate heat more rapidly by moving into shaded microsites. I predicted that, at high air temperatures, the smaller species will shuttle between microsites more than larger species. I further predicted that foraging effort will be more greatly reduced in larger birds at high temperatures and thus larger birds will experience more severe foraging-thermoregulation trade-offs than smaller birds. Alternatively, larger birds have greater thermal inertia and thus might be able to endure elevated temperatures and remain active for longer than smaller birds. In addition, Czenze et al. (2020) show that drinking species have a greater evaporative cooling capacity and subsequently a higher heat tolerance than non-drinking species, therefore I predict that drinking larks should have to dissipate heat at low temperatures and remain in the in sun at higher air temperatures compared to non-drinking species. My aim was first to estimate the thermal landscape available to the larks

and other small passerines at my study site and then to quantify whether body size or drinking dependency influences their behaviour and utilization of available microsites.

Materials and Methods

a. Study site

The Tankwa Karoo basin is bordered by the Roggeveld escarpment in the east, the Klein Roggeveld in the southeast and Cederberg to the west (Rubin 1998; Mucina et al. 2006). The study took place in the Tankwa Karoo National Park (S32°14'27.9" E20°05'44.5"), which is situated in the northern region of the basin on the border between the Western and Northern Cape Provinces, 110 kilometres north of Ceres and 90 kilometres south of Calvinia (Rubin 1998; Bester et al. 2012; Figure 1). The park consists of 143 600 ha of Succulent Karoo biome which is a biodiversity hotspot (Mucina et al. 2006; Bester et al. 2012). Deemed to be a rain shadow desert, this region is one of the hottest and driest areas in South Africa, with air temperatures reaching up to 44 °C in summer, and receiving an annual rainfall of between 70 - 110 mm (Mucina et al. 2006; Esler et al. 2015). The landscape comprises extensive flat gravel plains, sandy washes and elevated ridges (Mucina et al. 2006). For the most part, the plains are very sparsely vegetated and are characterised by low succulent shrubland (Mucina et al. 2006). The study was conducted exclusively in the gravel and sandy alluvial plains regions of the Tankwa Karoo National Park (Figure 1), where the landscape is stark and the potential for behavioural trade-offs most apparent. The field work was conducted from the 29th October 2019 to 9th December 2019. At the time of the study, the Tankwa Karoo had been in a four-year drought.

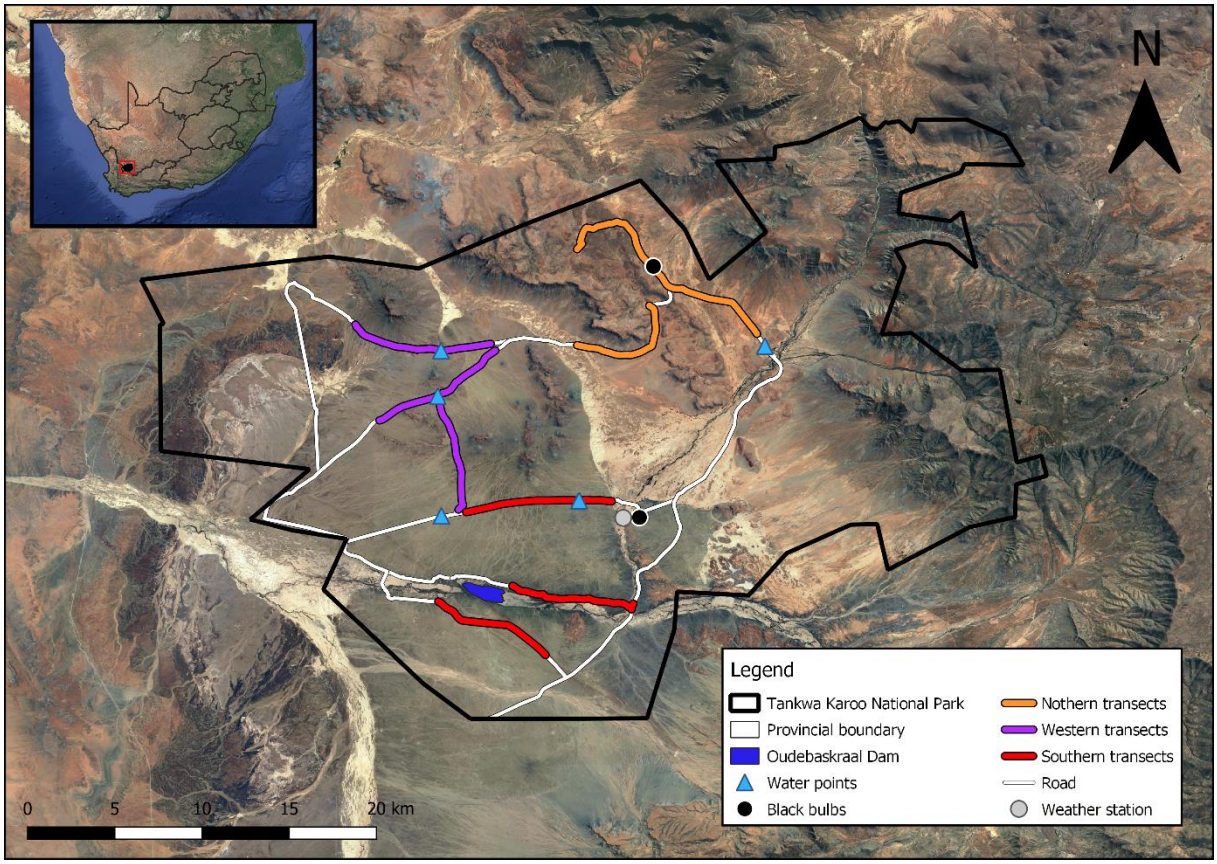

Figure 1 Satellite image of the study region within the Tankwa Karoo National Park, South Africa (Google Satellite: Imagery © 2020 TerraMetrics). The map shows park and provincial boundaries, transects, roads, water points, weather station and the location of black bulb arrays. Each black bulb symbol indicates the location where six black bulbs were deployed (six on gravel and six on sand). The inset map shows the location of the Tankwa Karoo National Park (marked by a red square) in South Africa.

b. Study species

Larks (Alaudidae) are a family of small, dull-coloured, ground-dwelling passerine birds that are distributed throughout Africa, Asia and Europe (Vaurie 1951). Larks are particularly well-represented in arid and semi-arid regions (Vaurie 1951; Dean & Hockey 1989). Of the 31 species found in southern Africa, 17 are found in the Karoo, with as many as eight lark species recorded in the Tankwa Karoo National Park (Dean 1995; Hockey et al. 2005; Animal Demographic Unit 2019). Only the most common resident species were included in this study: Red-capped Lark *Calandrella cinerea,* Spike-heeled Lark *Chersomanes albofasciata,* Karoo Lark *Calendulauda albescens* and Large-billed Lark *Galerida magnirostris.* There is a two-fold difference between the lightest (Red-capped Larks; 24 g) and the heaviest (Large-billed Larks; 45 g) larks in this group (Dean 2005b, 2005a). Spike-heeled Larks and Karoo Larks are intermediate in terms of body mass, weighing 25 g and 29 g respectively (Dean 2005c; Dean & Ryan 2005b). All four species are ground-foraging (Dean 2005b, 2005a, 2005c; Dean & Ryan 2005b). Their diet consists mostly of arthropods, seeds and fruit with the majority of the food intake being insects (Willoughby 1971; Dean & Hockey 1989). Spike-heeled and Karoo Larks do not drink, but obtain their primary sources of water from insects and metabolic water production (Willoughby 1971; Dean & Hockey 1989); whereas Red-capped Larks and Large-billed Larks rely on drinking surface water from dams and springs (Dean 2005b, 2005a). The four lark species also vary in their degree of sociality with Karoo and Large-billed Larks present in pairs, Red-capped Larks in mobile gregarious flocks that range from five to 20 individuals and Spike-heeled Larks forming family groups of three to five individuals (Dean 2005b, 2005a, 2005c; Dean & Ryan 2005b).

Other passerines were included in this study in order to provide an outgroup of different ecologies (but similar drinking behaviour) to compare larks against. These species were: Rufous-eared Warbler *Malcorus pectoralis* (10 g), Yellow Canary *Crithagra flaviventris* (17 g), Tractrac Chat *Cercomela tractrac* (24 g), White-throated Canary *Crithagra albogularis* (27 g) and Karoo Chat *Cercomela schlegelii* (32 g; (Dean 2005d, 2005e, 2005f, 2005g, 2005h). The majority of these species are insectivorous, however, their diet may also consist of seeds and fruit (Hockey et al. 2005). Both canary species drink surface water, while the remaining passerines do not (Hockey et al. 2005). These species are generally found by themselves or in

pairs, except for both canary species that can be found in small to large family groups (Hockey et al. 2005).

c. Black bulb and air temperature

Air temperature (°C), rainfall (mm), wind speed (km/h) and humidity (%) were measured by an onsite weather station (Vantage Pro2, Davis Instruments, Hayward, California, USA) installed on a pole 2 m off the ground and recording at 10-minute intervals.

I measured the black bulb temperature variation in the landscape using black bulb thermometers (hereafter black bulbs). These consisted of two copper hemispheres 30 mm in diameter and 1 mm thick, approximating the thoracic depth of a small bird. A Maxim Thermachron iButton^{TM} temperature logger (model DS1922L, Fairbridge Technologies, Sandton, South Africa) was enclosed within the two half-spheres which were then sealed together with superglue and subsequently painted matt black (following Bakken et al. 1985). The black bulbs were deployed at the start of the study and were programmed to log temperatures (to three decimal places) at 10-minute intervals for the entire duration of the field work. In total 12 black bulbs were deployed, six on gravel and six on sandy substrates. Each substrate had two replicate black bulbs placed in three representative microsites: “shade-ground”: in shade under a bush (ground level); “sun-bush”: in the sun on top of a bush (~60 cm off ground); and “sun-ground”: in the sun on the ground. The black bulbs were placed to capture approximate black bulb temperatures for a bird behaviourally thermoregulating by sitting in the shade, a bird sitting at the top of bush and lastly a bird that is in the open on the ground as if it were foraging.

Black bulbs are influenced by three of the factors that influence an organisms’ heat balance, namely: convective heat exchange, dry-bulb temperature and radiant heat exchange (Hetem et al. 2007; Mitchell et al. 2018). Therefore, they give a more accurate estimate of the thermal landscape available to small birds than measuring air temperature alone (Cunningham et al. 2015). Black bodies have an emissivity of one, with most feathers emitting infrared wavelengths of close to one (Mitchell et al. 2018); meaning that black bulbs are a fairly accurate proxy for feathers, although they lack the three-dimensional structure of a feathered

integument. However, black bulbs do not give a precise representation of thermoregulatory challenges experienced by the specific lark species, as they fail to capture the physical characteristics of the bird (e.g. body size and posture) as well as the influence of variables such as evaporation and humidity (Bakken et al. 1985; Cunningham et al. 2015). Therefore, black bulbs give an approximation which can be compared among different microsite locations and with air temperature, rather than recording the precise black bulb temperatures experienced by the birds.

d. Transects

I collected data on bird behaviour during three different time periods across the hottest part of the day (between 8:30 and 18:00) when there was the highest possibility that the behaviour of the birds would be affected by high temperatures (following Smit et al. 2016). The three different time periods were as follows: morning (8h30-11h00), early afternoon (12h30-15h00) and late afternoon (15h30-18h00). Therefore, a maximum of two and a half hours was spent searching for birds during each session.

Nine 8-kilometre transects were measured and marked in a GPS (Figure 1). All transects were plotted in such a way that they were at least 500 metres away from each other and 500 metres from the closest water source (following Martin et al. 2015; Smit et al. 2016). If a water point fell within the transect, the section of the transect that was within 500 metres of the water point was excluded and the equivalent distance was added on at the end of the transect. The transects were grouped into three sections, each section consisting of three transects in relatively close proximity. I conducted one section per day, randomizing the time period in which each transect was performed. A composite of driving and walking transects were used in order to locate birds for focal observations and scan samples. Driving transects were completed by moving at an average speed of 10 kilometres per hour. If no bird had been seen for more than a kilometre or the entire transect had been completed (and the full two and a half hours had not yet elapsed), the car was stopped and I began walking transects perpendicular to the main road transect in search of birds. I walked a minimum 100 metres away from the road before recording birds (to prevent pseudo-replication) and walked to a maximum of one and a half kilometres. Driving transects were the preferred method of

searching for birds as birds were more visible from the vehicle than on foot (Smit et al. 2016). Each transect was repeated at least three times for each time period (morning, early afternoon and late afternoon). The timing of the transects was arranged to ensure that each was performed evenly across the different times of the day. Transects were repeated every two days (not repeated on consecutive days to reduce the influence of observers on the behaviour of birds in subsequent transects).

e. Bird observations

Behaviour data were recorded using CyberTracker (CyberTracker 3.507), with a custom-built database created for this study. I worked together with a field assistant to collect data: one observer watched the focal bird with binoculars or a telescope and called out behaviour and the other entered the information on Cybertracker. If the presence of the observers altered the behaviour of the birds in way (e.g. flushed the bird or caused alarm calls), then the bird was given two minutes to resume normal behaviour after which, if the bird still was agitated, data were not recorded. If the bird was found in a group, such as was common with Spike-heeled Larks, then one of the individuals was randomly selected to be the focal individual.

i. Instantaneous scan samples

Instantaneous scan samples were conducted as per Altmann (1974). Scan samples were performed on every bird that was encountered during transects, regardless of species. Scan samples represented a “snapshot” in time of the bird’s behaviour at the moment it was encountered. Within each scan sample, I recorded the activity state of the bird (inactive = 0 or mobile = 1), exposure to the sun (shade = 0 or full sun = 1), the substrate type (e.g. sandy, gravel, rocky), whether the bird was foraging, on or off the ground and the type of shelter that was being used by the bird when in the shade (following methods of Smit et al. 2016).

ii. Focal observations

Focal observations as described by Altmann (1974) were conducted on every individual lark encountered, and were started immediately following the completion of scan sample data collection. Birds were observed continuously for 10 minutes. If the focal bird disappeared out of sight for more than two minutes at any point during the focal observation, then the focal observation was abandoned. Within the focal time period, each of the following behaviours were recorded: foraging, heat dissipation, social, breeding-related, singing, preening, scanning, and microsite use, as defined below.

Birds were considered to be foraging if they were seen handling prey, gleaning, digging or probing within the substrate or walking along the ground visually inspecting surfaces (du Plessis et al. 2012; Edwards et al. 2015). The time spent performing these behaviours was classified as foraging effort. Foraging intensity was the number of pecks, probes or digging motions made per minute spent foraging by the birds. Birds were described as exhibiting heat dissipation behaviour if they were panting or wing drooping (du Plessis et al. 2012). Panting occurred if a bird kept its beak open for more than 10 seconds without making any vocalisations. Wing drooping was defined as when birds hold their wings away from their body or droop them towards their feet (du Plessis et al. 2012). Panting and wing drooping frequently occurred simultaneously with other behaviours such as foraging. Scanning and resting behaviour were grouped as stationary behaviour, in which the bird remained motionless for extended periods of time and made no attempt to forage. Social behaviour was recorded as any interaction with other conspecifics. Any behaviour associated with nest building, maintenance and care was defined as breeding related activity.

Characteristics of the microsites in which behaviours occurred were also recorded, which included the exposure to the sun (shade or sun), position in relation to vegetation (under a bush, on top of a bush or open ground) and the position relative to the ground (on or off the ground, height estimated to the nearest 10 cm). To assess the birds' potential use of shuttling thermoregulation (moving between warmer and cooler microsites), the number of transitions between microsites was also recorded. To determine the influence of microsite, use and heat dissipation behaviour on foraging intensity, the number of pecks, probes or digging motions

made by the bird was logged when foraging while heat dissipating and when foraging in different microsites.

f. Statistical analyses

All statistical analyses were performed in the R statistical environment version 3.6.2 (R Core Team 2019), using the interface R Studio (RStudio Team 2016). Previous studies have highlighted the influence of humidity on evaporative cooling capability and heat load in birds (Smit et al. 2013; Gerson et al. 2014). For example, White-browed Sparrow-Weavers were found to have higher body temperatures at vapour pressure deficits < 2 kPa (Smit et al. 2013). Similar to Pattinson et al. (2019), vapor pressure deficits below 2 kPa consisted of only a minor proportion of my data. As a consequence, all observations were included irrespective of humidity (following Smit et al. 2016; Pattinson et al. 2019). All body mass values were obtained from Hockey et al. (2005), while drinking dependency (whether or not the species drink) was obtained from Willoughby & Cade (1967), Willoughby (1971) and Hockey et al. (2005).

i. Black bulb temperature

Black bulb temperatures were averaged for all replicate black bulbs within each of the three microsites: sun-ground, shade-ground and sun-bush, and linear models (LMs) with gaussian error distribution were used to assess the relationships between black bulb temperature and air temperature (recorded by the weather station), and black bulb temperature and time of day in each microsite, and on sandy versus gravel substrates. Preliminary data exploration suggested that black bulb temperatures might have a quadratic relationship with air temperature. Therefore, I used Akaike's Information Criterion (AIC) score to determine whether the best-fitting models for the relationships between black bulb and air temperature in each microsite included air temperature as a linear or quadratic term. For all microsites, the models with a quadratic term for air temperature had a lower AIC score (<2) than those with only a linear term. Model estimates are presented ± 1 SE, unless otherwise stated.

I used analyses of variance (ANOVA) to compare the black bulb temperatures in each microsite within and between each substrate type. A post hoc test was performed using the ghlt function in the multcomp package (Hothorn et al. 2019) to make multiple comparisons.

ii. Instantaneous scan samples – all passerines

Generalised linear mixed models (GLMMs) with binomial error distribution in the glmmADMB package (Fournier et al. 2016) were used to fit a logistic regression on the presence or absence of heat dissipation (panting and wing-drooping), shade-seeking (whether in the sun or the shade), activity (active versus inactive) and foraging (foraging versus not) as a function of air temperature for all four lark species, and for the five additional passerine species for which I was able to collect sufficient data (n > 20 observations). I included the random factor transect to account for likely repeated measures of the same individual birds along the same transects. I estimated the air temperature when the behavioural response occurred in half (50%) of all observations for each species (e.g. heat dissipation (HD_{50}), shade-seeking ($shade_{50}$), activity (act_{50}) and foraging (for_{50})) by dividing the absolute value of the intercept by the absolute value of beta-estimate of each species-specific model, following Smit et al. (2016). I then performed Pearson's correlation tests to determine the relationship between body mass and HD_{50}, $shade_{50}$ and for_{50} for larks and for the nine passerine species together. Comparisons between drinking and non-drinking species were made using paired t-tests.

iii. Focal observations - larks

Time budgets: I fitted GLMMs with binomial error distribution to examine the relationship between air temperature and time budget data (time spent engaged in heat dissipation, shade-seeking, activity, foraging and height seeking (moving from ground level to areas off the ground)) extracted from focal observations of the four lark species, using the lme4 package (Bates et al. 2015). Heat dissipation was modelled as a combined vector of "total time engaged in heat dissipation behaviour (seconds)" compared to "total time not heat dissipating (seconds)"; shade-seeking was modelled as a combined vector of the "total time spent in the shade (seconds)" compared to "total time spent in the sun (seconds)"; foraging effort was modelled as a combined vector of "total time spent foraging (seconds)" compared

to “total time engaged in non-foraging behaviours (seconds)” and height seeking was modelled as a combined vector of “time spent off the ground (seconds)” compared to “time spent on the ground (seconds)”. Because time budgets could also be affected by time of day, whether the birds were approached by vehicle or on foot, and whether they were in gravel or sandy substrates, I applied a model selection approach, by fitting a global model with four fixed factors (air temperature, time of day, transect type and substrate type) and “transect” as a random factor. I also included an observation-level random factor (“focal ID”) to control for overdispersion (following Harrison 2014). A candidate set of models nested within the global model, all of which included air temperature as a fixed factor (as this was the main predictor variable of interest) except for the null model, were compared using the MuMIn package (Barton 2019). Best-fitting models were identified using Akaike’s Information Criteria corrected for small sample sizes (AICc). If more than one model was within two AICc points of the top model, then model averaged coefficients for the top model set are presented. All time budget models were fitted using the optimiser “bobyqa” to aid model convergence, and the continuous air temperature variable was scaled. Similarly, all models were weighted by “time in sight”, giving longer focal observations (which might provide a more accurate sample of the birds’ behaviour over time) more weight than shorter focal observations. Models that did not converge were excluded from the analysis (Appendix D). Small sample sizes for walking transects (n = 3) and sandy substrates (n = 2) for Large-billed Larks meant that I was unable to investigate an effect of substrate and transect type. As a result, these factors were excluded from all time budget models for this species.

Transitions: GLMMs using glmmADMB package (Fournier et al. 2016) were used to model the number of transitions focal birds made between sunny and shaded microsites, and between on-ground and off-ground microsites, within each focal. Only focal observations longer than five minutes were included in these analyses, because on visual inspection of the majority were longer than five minutes and focal observations less than five minutes added excessive variation. Because these count data were sometimes zero-inflated, a model selection approach using MuMIn (Barton 2019) was used to determine the best-fitting error structure for each species, comparing global models including five fixed factors (air temperature, quadratic air temperature term, time of day, transect type and substrate type) and “transect” as a random factor. As with the time budget analysis, an observation-level random factor

("focal ID") to control for overdispersion was also included (following Harrison 2014). These models also included the offset "total time in sight (minutes)" that was logged to account for the fact that the duration of each focal observation varied in length. Air temperature was included as a quadratic term, because preliminary data exploration suggesting that a quadratic relationship was present between these transitioning behaviours and air temperature. Error structures included in the model selection were: Poisson, negative binomial, negative binomial (zero-inflated), negative binomial "type 1" and negative binomial "type 1" (zero-inflated; Appendix E). The error distribution yielding the lowest AIC was considered the most robust and was used in subsequent models for that species. If the error structure model with the lowest AIC was over-dispersed, the model with the second lowest AIC score was selected. Once the error structure was selected, I used the same model selection approach as that performed in the time budget analysis. As in the case of time budget data, walking transects, and sandy substrates for Large-billed Larks were excluded from the transition models due to their small sample sizes. Small sample sizes for observations in the early afternoon (n = 2), sandy substrates (n = 2) and walking transects (n = 3) for Red-capped Larks meant that I was unable to investigate an effect of time of day, substrate and transect type. Therefore, all fixed factors except for air temperature were removed from the candidate model set for Red-capped Larks.

A Kruskal-Wallis test was fitted to all lark data to determine whether there were differences in the number of transitions between sunny and shaded microsites per focal observation between species, and a pairwise Wilcoxon rank sum test was used to identify which species were significantly different from one another.

To determine the influence of heat dissipation behaviour and microsite use on foraging intensity (number of pecks per minute foraging), I ran paired Wilcoxon signed rank tests on data comparing peck rates in sunny versus shaded microsites, and when the bird was heat dissipating versus not within the same focal observations on the same birds. Data were selected by only including focal observations within which birds were observed foraging in both sunny and shaded microsites (for microsite analysis; Red capped lark n = 3, Spike-heeled Lark n = 59, Karoo Lark n = 59, Large-billed Lark n = 7); or foraging without simultaneously heat-dissipating and foraging while heat dissipating within the same focal observation (heat

dissipation analysis; Spike-heeled Lark n = 6). Using this method controlled for temperature and resource availability which are unlikely to fluctuate considerably within single focal observations (see du Plessis et al. 2012; van de Ven et al. 2019).

Results

In total, 86 transects were performed: 29 in the morning, 28 in the early afternoon and 29 in the late afternoon. Twenty-nine transects were completed in the northern (orange), 28 in the western (purple) and 29 in the southern section of the park (red; Figure 1). Observations were made over a range of air temperatures from 16.2 °C to 43.2 °C.

a. Black bulb temperature

Black bulb temperature was always greater than air temperature and increased significantly (all $p < 0.001$; Appendix A) with air temperature for all three microsites on both sandy and gravel substrates (Figure 2a). On average the temperatures recorded by the black bulbs were ~ 9 °C warmer than air temperature. The maximum air temperature observed in this study was 43.2 °C, while the maximum black bulb temperature recorded was 59.6 °C. Black bulb temperatures recorded on gravel substrates were significantly higher (all $p < 0.001$; Appendix B) than the corresponding microsites on sandy substrates, with the average across all microsites in the gravel regions of the park being 1.5 °C warmer than sand (Figure 3).

When comparing black bulb temperatures within each substrate type, all microsites differed significantly from one another (all $p < 0.01$; Appendix A). The warmest microsite in both substrate types was in the sun on the ground. The sun-ground microsite reached its maximum temperature earlier in the day than the other two microsites (Figure 2b). Microsites on the ground in the shade were consistently the coolest available locations on the sandy substrate, while on the gravel, shade-ground was the coolest microsite for air temperatures less than 31 °C, after which the sun-bush microsite became the coolest microsite. There was a significant interaction (all $p < 0.05$; Appendix C) between microsite and substrate type, which resulted in the black bulb temperature being significantly higher on gravel than on sand in both on-ground microsites; but similar in the sun-bush microsite.

A bird on the ground that transitioned from being in the sun to the shade would experience a decrease in black bulb temperatures of 4.10 - 8.16 °C for gravel and 3.96 - 7.94 °C for sand, with more considerable decreases in the morning and early afternoon compared with late

afternoon. A bird in the sun on the ground that moved to an off-ground sunny perch would experience a decrease in black bulb temperatures of 4.91 – 8.02 °C if on a gravel substrate and between 3.09 – 5.88 °C on sand. Overall, there were similar decreases in temperature between sun-ground and sun-bush microsites in the morning and late afternoon (~3 °C), however, the greatest decreases were observed in the early afternoon (5.88 °C).

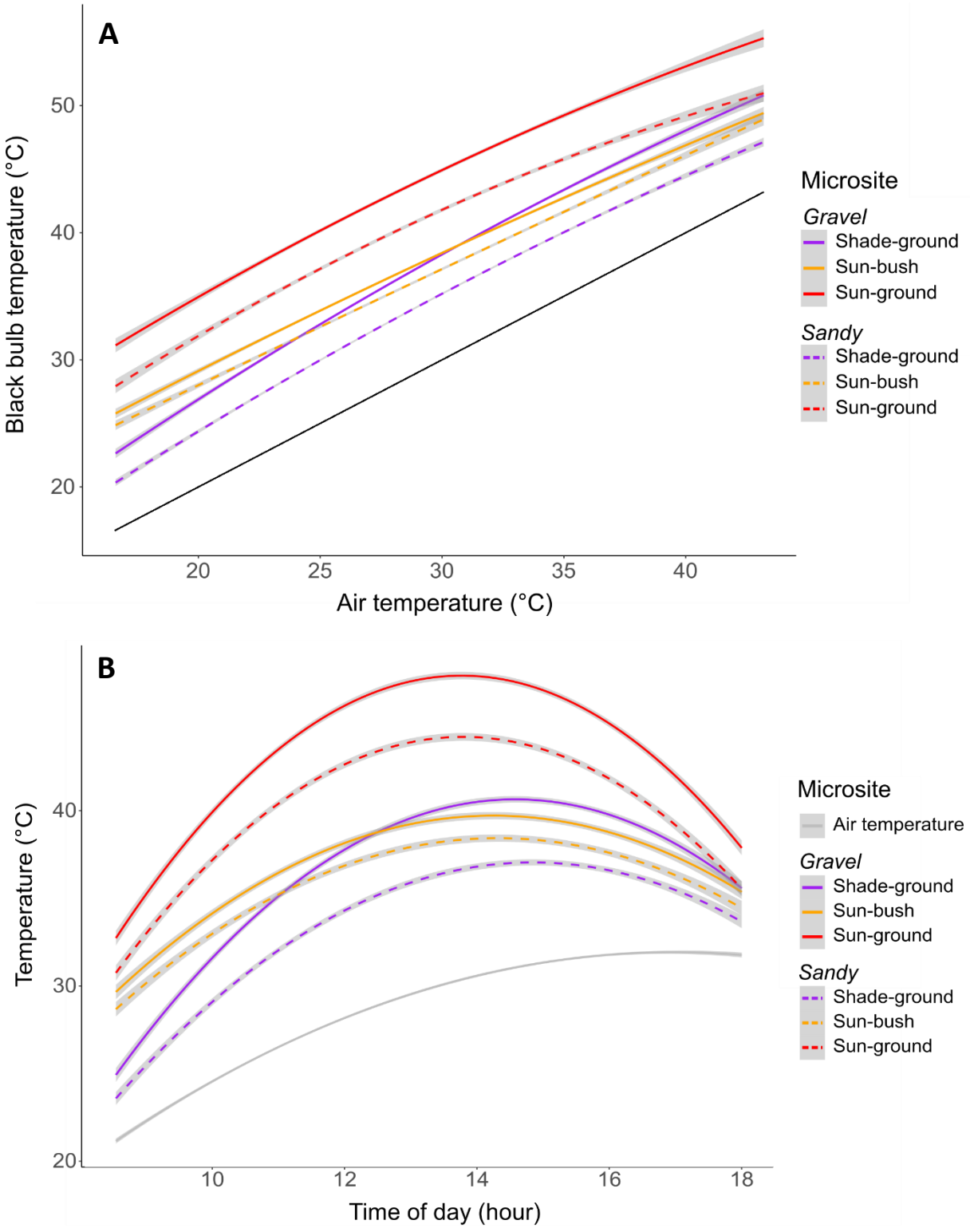

Figure 2 a) Black bulb temperature as a function of air temperature for each microsite on the different substrates, with the black line indicating where air temperature and the black bulb temperature are equal b) black bulb temperature and air temperature as a function of time of day (in hours) for each microsite on the different substrates.

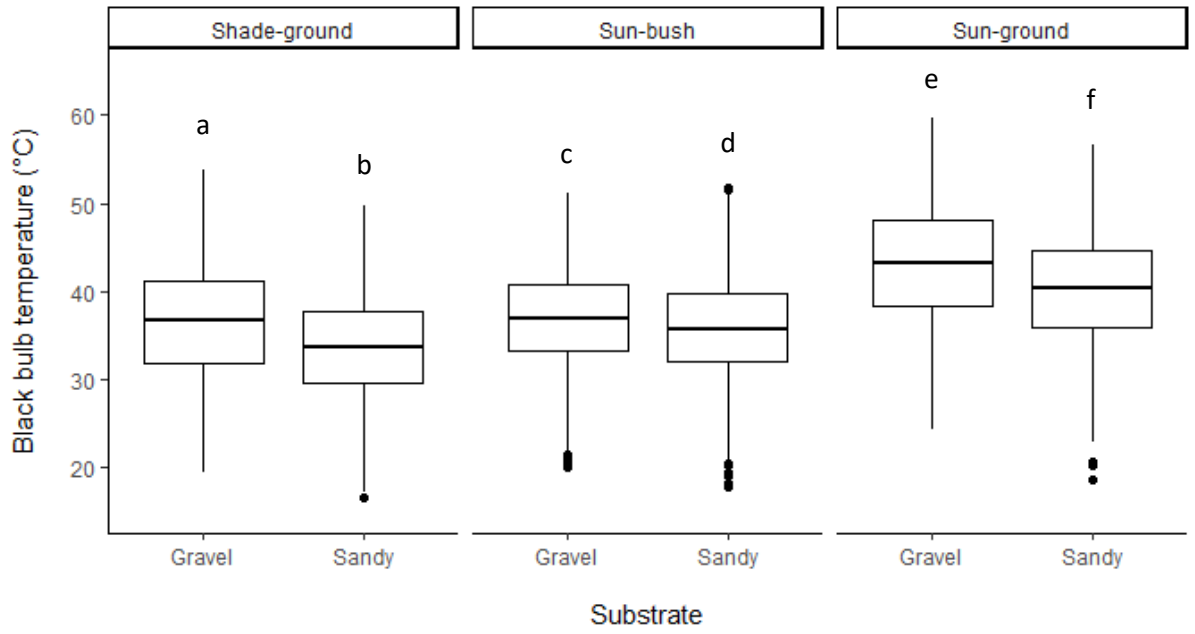

Figure 3 Boxplot comparing the black bulb temperatures measured in different microsites on gravel and sandy substrates, across all times of day. Different letters indicate significant differences between microsites (ANOVA and ghlt; $p < 0.01$).

b. Instantaneous scan samples

In total, 973 scan samples were recorded for nine passerine species throughout the duration of the study (Table 1). Eight of the nine passerines displayed heat dissipation behaviour and were observed in the shade, consequently the comparison between species for these behaviours includes only these eight species.

Table 1 All passerines recorded in the study, their mass in grams according to Hockey et al. (2005), drinking dependency (whether they drink (D) or not (ND)), the relevant literature where drinking dependency was cited from, and sample size for scan samples and focal observations for each species.

Species	Mass (g)	D/ND	Reference for drinking dependency	No. of scans	No. of focals
Tractrac Chat	24	ND	Willoughby & Cade 1967 *	444	
Karoo Lark	29	ND	Willoughby 1971	154	80
Spike-heeled Lark	25	ND	Willoughby 1971	110	76
Karoo Chat	32	ND	Willoughby & Cade 1967 *	97	
Yellow Canary	17	D	Dean 2005f	52	
Large-billed Lark	45	D	Dean 2005a	42	27
Rufous-eared Warbler	10	ND	Willoughby & Cade 1967 *	37	
White-throated Canary	27	D	Dean 2005g	22	
Red-capped Lark	24	D	Dean 2005b	15	15

*Species were classified as seldom drinking according to the study

i. Comparisons between drinking and non-drinking passerines

There was no relationship between body mass and HD50 for all passerines. However, drinking passerines had a significantly lower HD_{50} than the non-drinking species (t = -3.25, df = 4.63, p-value = 0.025; Figure 4a). This pattern was reflected within the four focal lark species: both non-drinking larks had higher HD_{50} than drinking larks (Figure 4b).

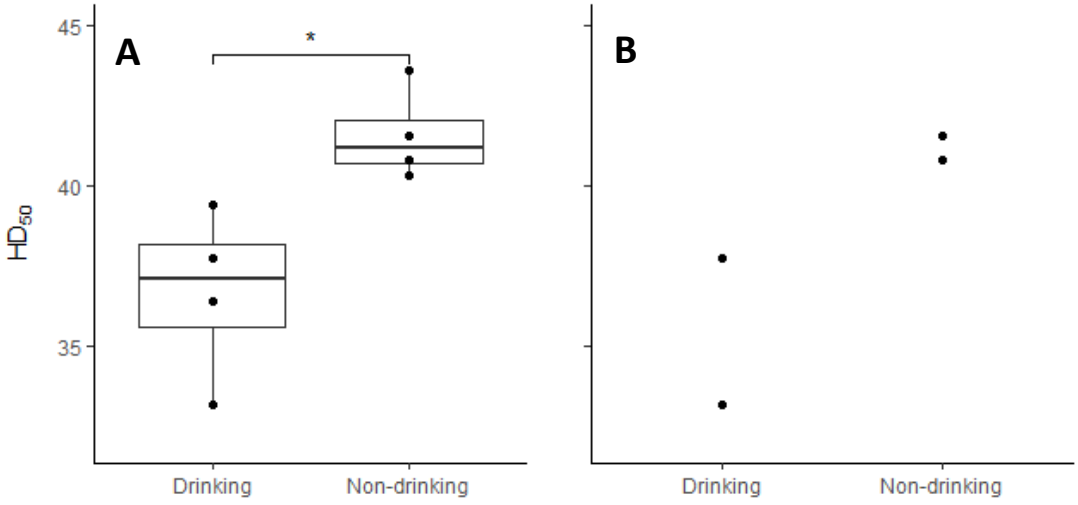

Figure 4 Boxplot comparing HD_{50} values (an estimate of air temperature when heat dissipation occurred in half (50%) of all observations for each species) between drinking and non-drinking a) passerines (including larks) and b) larks. Asterisk (*) indicates significance between the two groups (t-test; $p < 0.05$).

There was a non-significant relationship between body mass and $shade_{50}$ for all passerines. Similarly, drinking and non-drinking species did not differ significantly in $shade_{50}$ overall, however both non-drinking larks had lower $shade_{50}$ values than the two drinking larks (Figure 5). Both drinking larks (Large-billed Lark and Red-capped Lark) had $shade_{50}$ values ~40 °C, whereas the non-drinking Spike-heeled and Karoo Larks had $shade_{50}$ values of 35 °C and 31 °C respectively.

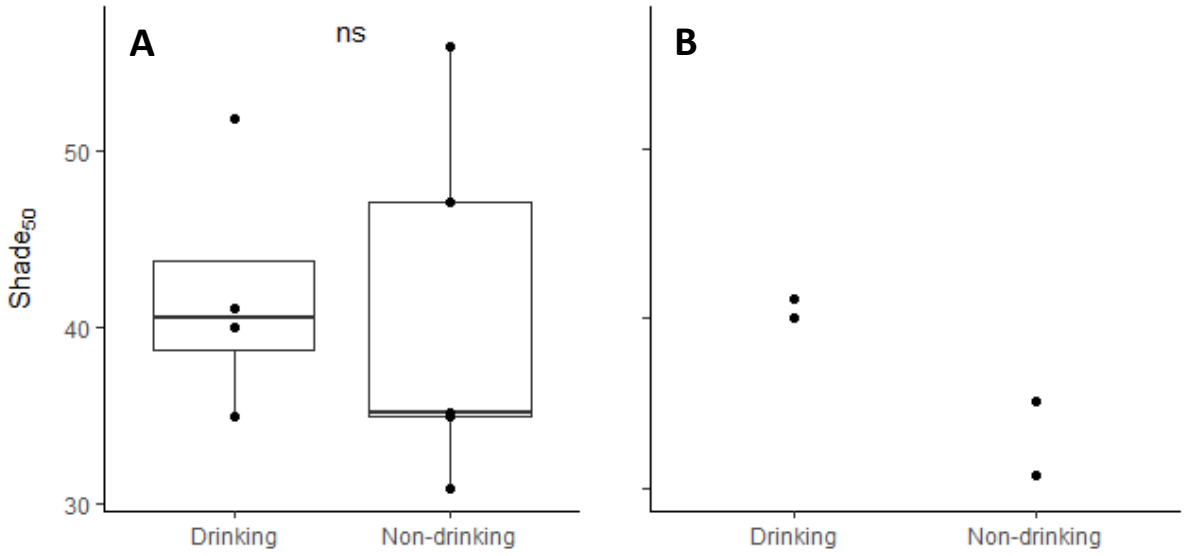

Figure 5 Boxplot comparing $shade_{50}$ values (an estimate of air temperature when shade-seeking occurred in half (50%) of all observations for each species) for non-drinking and drinking a) passerines (including larks) and b) larks. Asterisk (*) indicates significance between the two groups (t-test).

Act_{50} and for_{50} data were correlated ($t = 22.35$, $df = 7$, p-value < 0.001). Furthermore, for all lark species, foraging behaviour contributed between 96 and 100% of scan sample observations where the bird was considered to be active. Foraging behaviour was used as a proxy for activity, because it provides a more direct measure of the effects that temperature has on trade-offs between foraging and thermoregulation. There was no significant relationship between for_{50} and body mass across the nine passerine species. However, within the four larks, there was a strong ($r = 0.84$), but non-significant negative relationship between for_{50} and body mass ($t = -2.23$, $df = 2$, p-value = 0.16).

ii. Comparisons between the four lark species

As air temperature increased, the frequency of heat dissipation increased significantly for Spike-heeled Larks (Est. 0.17 ± 0.07, z-value 2.46 , $p < 0.05$) and Karoo Larks (Est. 0.21 ± 0.06, z-value 3.78, $p < 0.001$), while there was no significant influence of temperature on heat dissipation for the other two species (Figure 6). Likewise, there was a significant shift in microsite, with Spike-heeled Larks (Est. -0.30 ± 0.08, z-value -3.70, $p < 0.001$) and Karoo Larks (Est. -0.18 ± 0.04, z-value -4.44, $p < 0.001$) moving from the sun into the shade at higher air temperatures than the drinking species (Figure 7). All lark species, except Red-capped Lark, showed reductions in foraging at high air temperatures (Spike-heeled Larks, Est. -0.113 ± 0.05, z-value -2.37, $p < 0.05$; Karoo Larks, Est. -0.18 ± 0.04, z-value -4.40, $p < 0.001$ and Large-billed Larks, Est. -0.13 ± 0.06, z-value -2.11, $p < 0.05$; Figure 8). Only Large-billed Larks moved off the ground significantly more as temperatures increased (Est. 0.14 ± 0.06, z-value 2.27, $p < 0.05$).

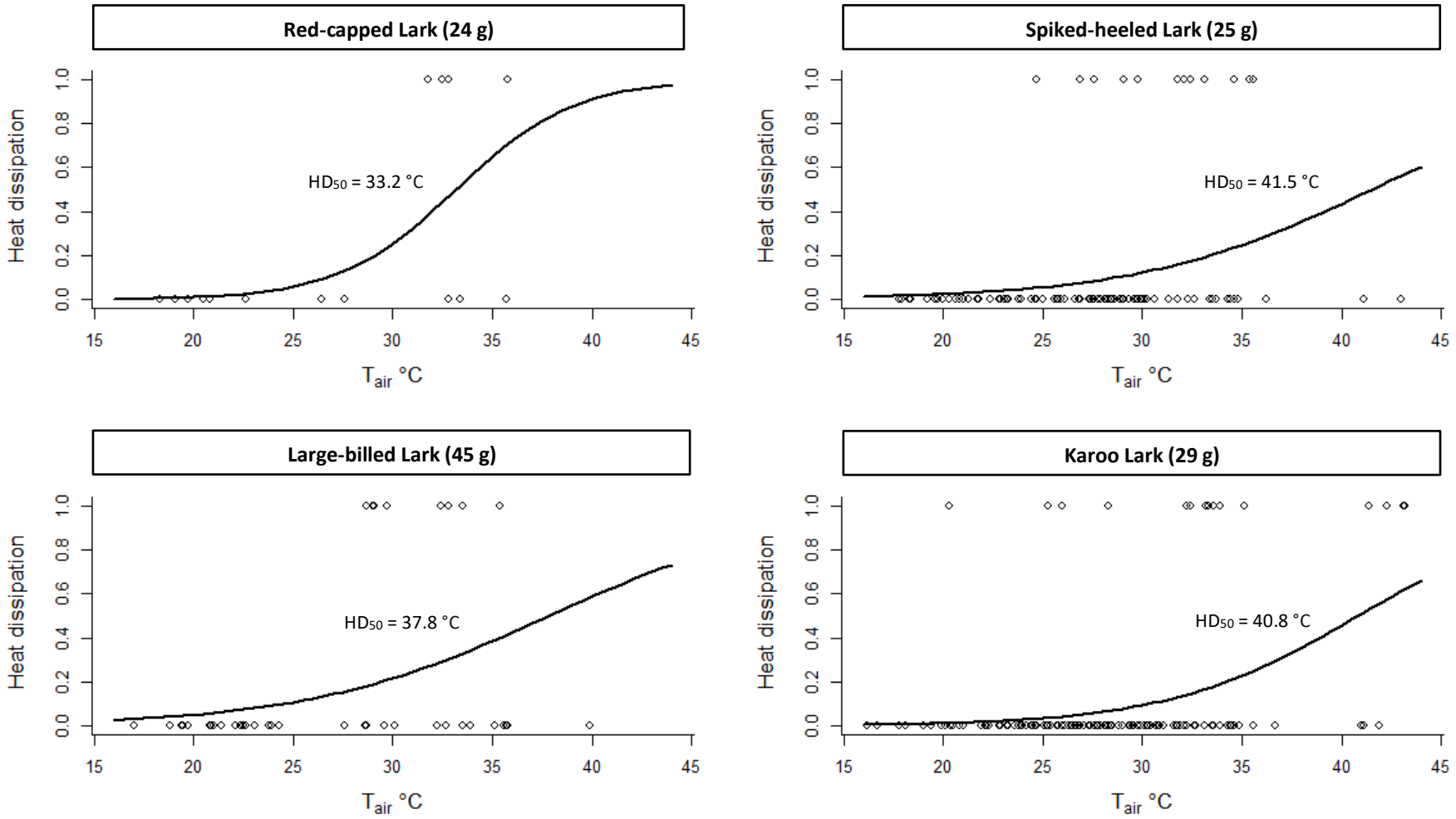

Figure 6 Logistic regressions demonstrating the probability of observing heat dissipation behaviour (presence =1, absence = 0) for Red-capped Lark (top left), Spike-heeled Lark (top right), Large-billed Lark (bottom left) and Karoo Lark (bottom right) as a function of air temperature (T_{air}). Regressions for Spike-heeled and Karoo Larks were statistically significant (both $p < 0.05$). Red-capped and Large-billed Larks are drinking species (left column) and Spike-heeled and Karoo Larks are non-drinking species (right column). Drinking species had lower HD_{50} values than non-drinking species.

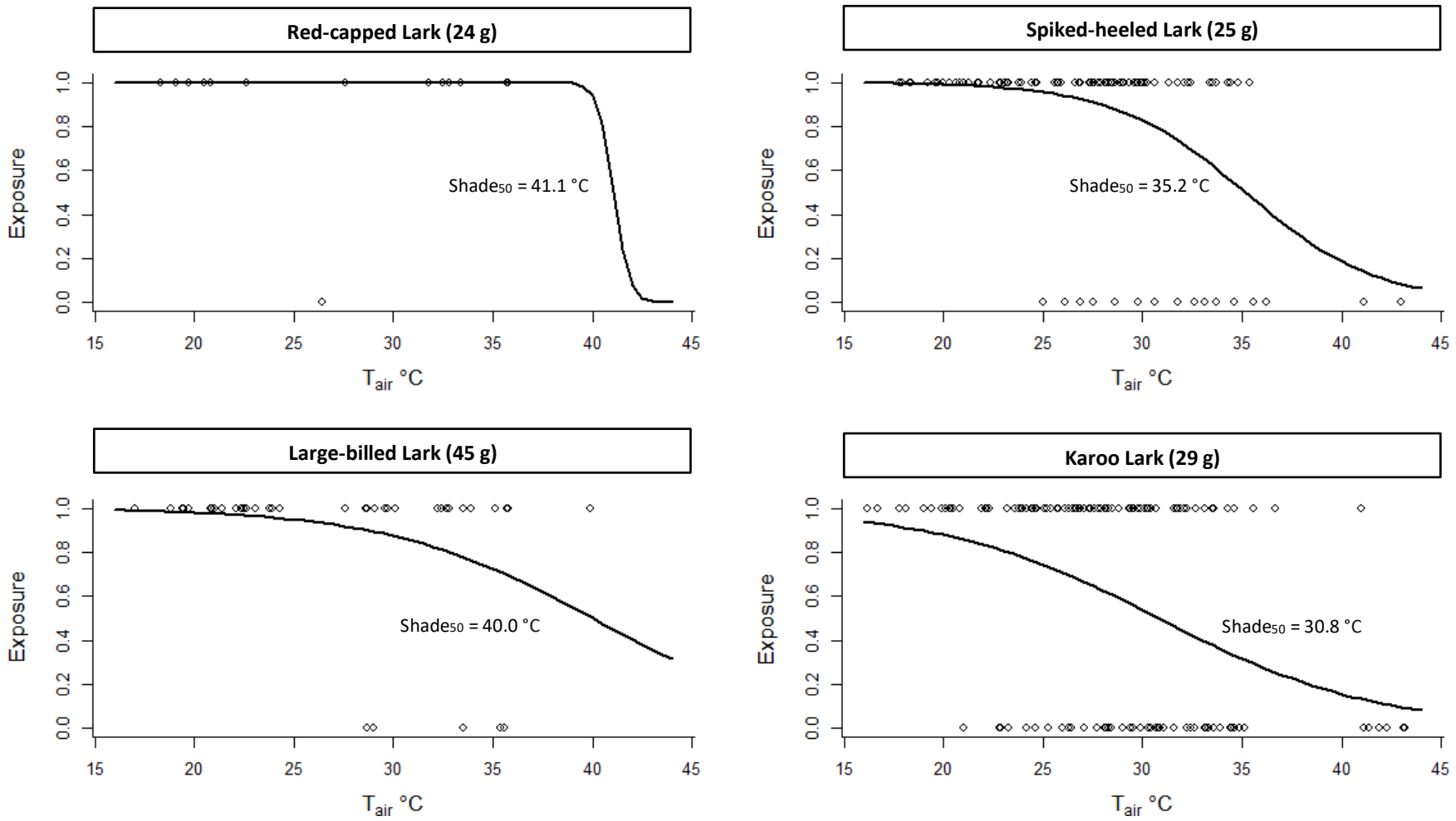

Figure 7 Logistic regressions demonstrating the predicted exposure (sun = 1, shade = 0) for Red-capped Lark (top left), Spike-heeled Lark (top right), Large-billed Lark (bottom left) and Karoo Lark (bottom right) as a function of air temperature (T_{air}). Regressions for Spike-heeled and Karoo Larks were statistically significant (both $p < 0.001$). Red-capped and Large-billed Larks are drinking species (left column) and Spike-heeled and Karoo Larks are non-drinking species (right column). Drinking Larks had a higher $shade_{50}$ than non-drinking species.

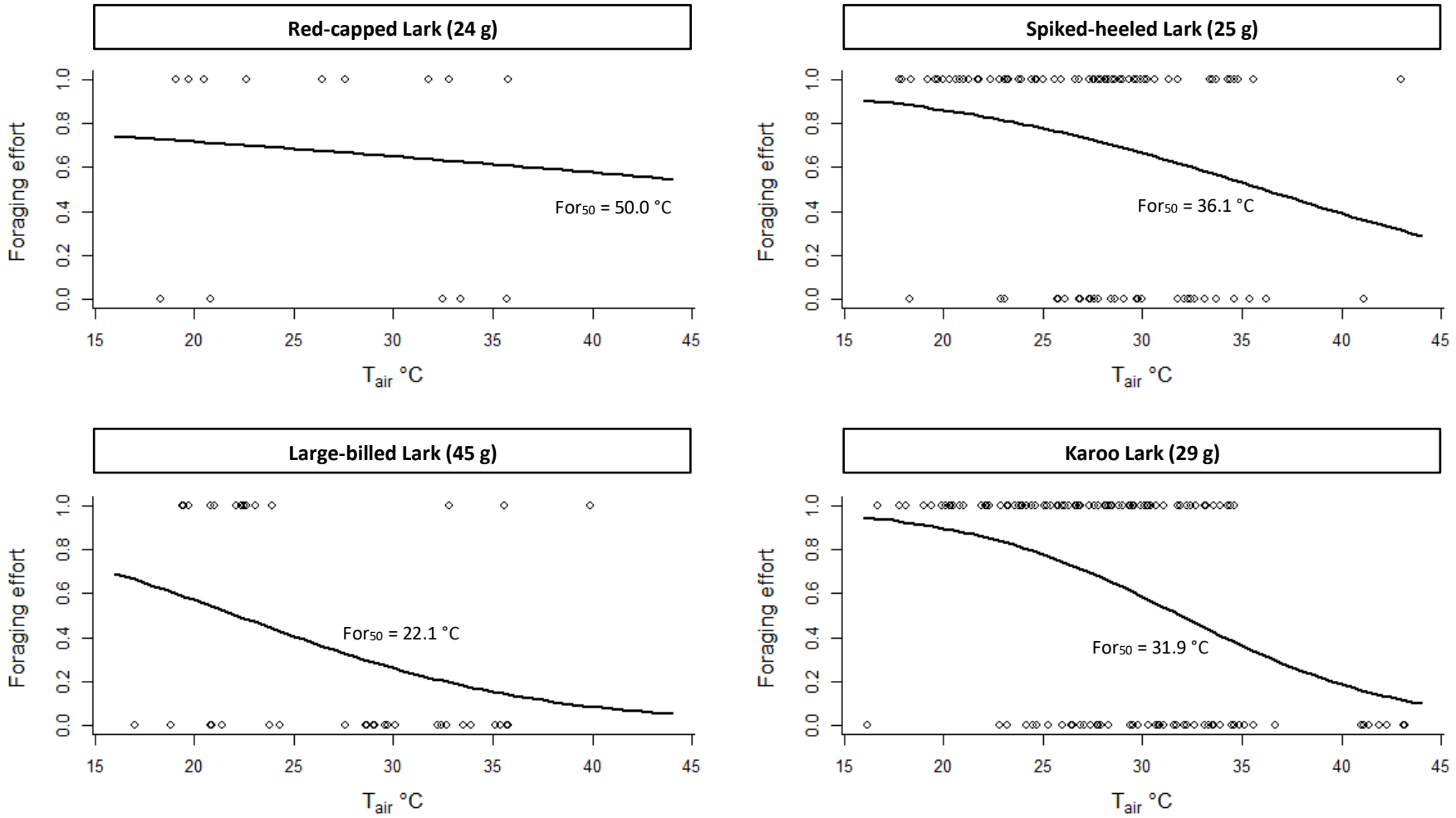

Figure 8 Logistic regressions demonstrating the predicted proportion of foraging behaviour (mobile = 1, stationary = 0) for Red-capped Lark (top left), Spike-heeled Lark (top right), Large-billed Lark (bottom left) and Karoo Lark (bottom right) as a function of air temperature (T_{air}). Regressions for all lark species, except Red-capped Larks were significant (all $p < 0.05$). Red-capped and Large-billed Larks are drinking species (left column) and Spike-heeled and Karoo Larks are non-drinking species (right column). Heavier larks had lower for_{50} values than lighter larks.

c. Focal observations

In total, I collected 198 focal observations on larks, comprising: Spike-heeled Larks (n = 80), Karoo Larks (n = 76), Large-billed Larks (n = 27) and Red-capped Larks (n = 15).

i. Time budget

The time spent engaged in heat dissipation behaviour significantly increased with temperature in Spike-heeled Larks (Table 2; Model-averaged Est. 8.40 ± 1.64, Adjusted SE 1.67, z-value 5.02, $p < 0.001$). The best-fit model for Karoo and Large-billed Larks included temperature, but the temperature effect was not significant. The null model was the best-fit model for heat dissipation time budgets of Red-capped Larks. Karoo Larks spent significantly more time in the shade with increasing temperatures (Model-averaged Est. 1.55 ± 0.50 Adjusted SE 0.51, z-value 3.08, $p < 0.001$). Best-fit models for time spent in the shade for Spike-heeled Larks and Large-billed Larks included temperature, but again the temperature effect was not significant. The null model was selected as the best-fit model for shade-seeking behaviour of Red-capped Larks. Spike-heeled Larks (Est. -1.10 ± 0.52, Adjusted SE 0.53, z-value 2.06, $p < 0.05$) and Karoo Larks (Est. -2.71 ± 0.62, z-value, -4.38, $p < 0.001$) spent significantly less time foraging as temperature increased; but air temperature did not have a significant influence on the time spent foraging for Large-billed Larks. The null model was selected as the best-fit model for Red-capped Larks. The best-fit model for the time spent off the ground for all the species, except Red-capped Larks, included temperature, although this was not significant. The null model was selected as the best-fit model for time spent off the ground of Red-capped Larks.

Overall, the significant results obtained in the time budget analyses from focal data, were also significant in the scan sample analyses. However, not all significant results obtained in the scan samples are reflected in the focal time budget analysis.

Table 2 GLMM fixed variables selected in the models (AICc < 2) that explain time budget for heat dissipation, shade-seeking, foraging and height-seeking behaviour for Red-capped, Spike-heeled, Karoo and Large-billed Larks.

Species	n	Number of best Model	Temp	Substrate type	Time of day	Transect type	df	AICc	delta	Weight
Heat dissipation										
Red-capped Lark	15	1		NI	NI	NI	3	25636.3	0.00	0.684
Spike-heeled Lark	76	3	8.409		+	+	7	96105.5	0.00	0.404
			8.057	+	+	+	8	96106.4	0.91	0.257
			8.776		+		6	96106.8	1.37	0.203
Karoo Lark	80	2					3	72381.0	0.00	0.475
			1.548				4	72382.1	1.12	0.271
Large-billed Lark	27	2		NI		NI	3	29695.7	0.00	0.677
			5.830	NI		NI	4	29697.4	1.68	0.292
Shade-seeking										
Red-capped Lark	15	1					3	22813.8	0.00	0.819
Spike-heeled Lark	76	2	0.472	+	+		7	260442.2	0.00	0.374
			0.419		+		6	260443.6	1.39	0.186
Karoo Lark	80	2	1.536			+	5	229011.9	0.00	0.357
			1.574	+		+	6	229012.1	0.22	0.320
Large-billed Lark	27	2		NI		NI	3	41372.5	0.00	0.641
			7.136	NI		NI	4	41374.1	1.57	0.293
Foraging										
Red-capped Lark	15	1					1	33994.3	0.00	0.806
Spike-heeled Lark	76	3	-1.118				4	260765.1	0.00	0.277
			-1.071		+		6	260765.4	0.27	0.242
			-1.103			+	5	260767.0	1.83	0.111
Karoo Lark	80	1	-2.710				4	216803.1	0.00	0.537
Large-billed Lark	27	3	-1.089	NI		NI	4	94815.6	0.00	0.493
			-1.961	NI	+	NI	6	94816.8	1.23	0.267
				NI		NI	3	94817.0	1.44	0.240
Height-seeking										
Red-capped Lark	15	1					3	16908.4	0.00	0.835
Spike-heeled Lark	76	5	1.665	+	+		7	214702.5	0.00	0.211
			1.567		+		6	214702.5	0.05	0.206
			1.177				4	214703.0	0.51	0.163
			1.191	+			5	214704.1	1.65	0.093
							3	214704.3	1.77	0.087
Karoo Lark	80	2					3	50838.3	0.00	0.527
			-0.855				4	50839.8	1.56	0.242
Large-billed Lark	27	2		NI		NI	4	55963.9	0.00	0.521
			3.103	NI		NI	6	55964.2	0.38	0.431

*NI – Not included in the model

ii. Number of transitions between the sun and shade

The number of transitions Spike-heeled Larks made between sunny and shaded microsites had a quadratic relationship with air temperature, first increasing then declining again as air temperature increased (Table 3; Model-averaged Est. -0.01 ± 0.00, Adjusted SE 0.00, z-value 2.13, $p < 0.05$). A similar relationship was observed in the number of transitions by Karoo Larks with respect to air temperature (Model-averaged quadratic temperature Est. 0.01 ± 0.00, Ad SE 0.00, z value 2.43, $p < 0.05$). For the two drinking species, Red-capped Larks and Large-billed Larks, there was no influence of air temperature on the number of transitions between sun and shade. Overall, drinking lark species shuttled between sun and shade less often compared to non-drinking species (Figure 9).

Table 3 GLMM fixed variables selected in the models (AICc < 2) that explain the number of transitions of larks between the sun and shade, and between on-ground and off-ground for Red-capped, Spike-heeled, Karoo and Large-billed Larks.

Species	N	Number of best Model	Temp	Temp^2	Substrate type	Time of day	Transect type	Df	AICc	delta	Weight
Transitions between sun and shade											
Red-capped Lark	15	2	0.2019		NI	NI	NI	4	74.2	0.00	0.575
					NI	NI	NI	3	75.0	0.78	0.390
Spike-heeled Lark	76	2	0.4458	-0.0075	+	+		8	529.3	0.00	0.340
			0.3849	-0.0063		+		9	530.3	1.01	0.205
Karoo Lark	80	2	0.4164	-0.0082		+		8	454.1	0.00	0.461
			0.4644	-0.0089		+	+	9	454.9	0.87	0.299
Large-billed Lark	27	1	0.6312	-0.0127	NI	+	NI	7	118.9	0.00	1
Transitions between on-ground and off-ground											
Red-capped Lark	15	2	0.1927		NI	NI	NI	4	52.7	0.00	0.630
					NI	NI	NI	3	54.0	1.29	0.331
Spike-heeled Lark	76	1						4	439.2	0.00	0.551
Karoo Lark	80	3	0.7302	-0.0163		+		8	142.8	0.00	0.326
			0.0876	-0.0188				7	143.5	0.67	0.233
			-0.1167					6	144.6	1.81	0.132
Large-billed Lark	27	1			NI		NI	4	129.7	0.00	0.743

*NI – Not included in the model

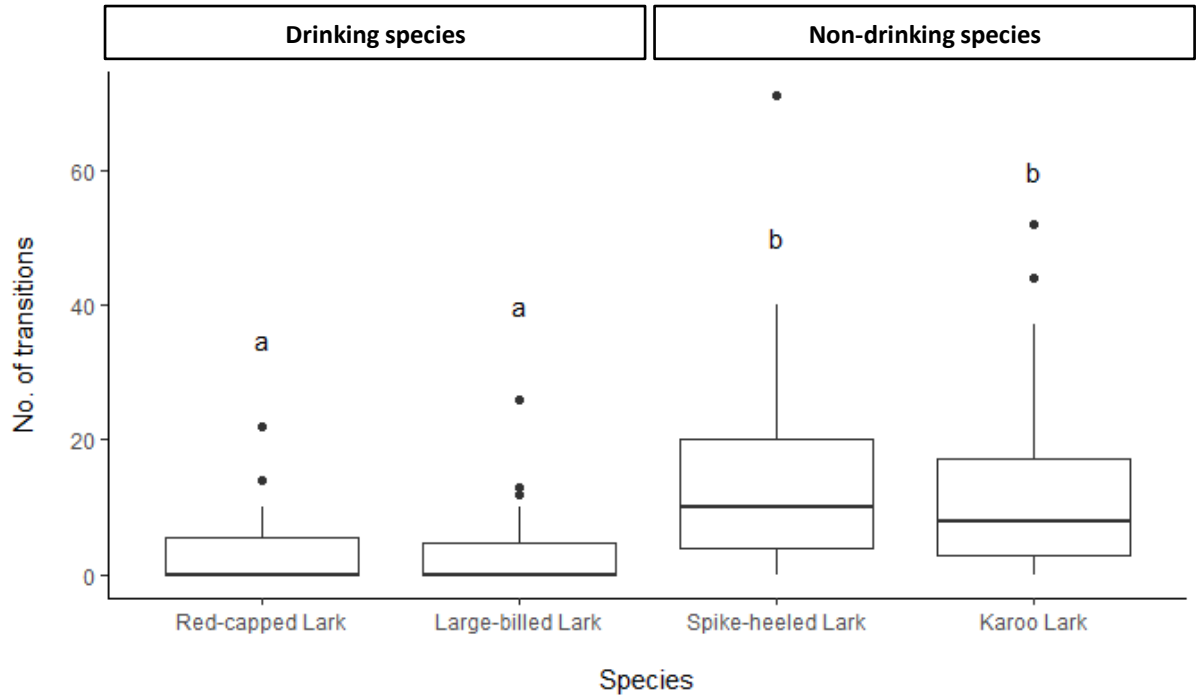

Figure 9 Boxplot comparing the number of transitions between sun and shade for all temperatures among Red-capped (n = 15), Large-billed (n = 26), Spike-heeled (n = 80) and Karoo Larks (n = 76). Different letters indicate significant differences between species (pairwise Wilcoxon rank sum test; $p < 0.05$).

iii. Number of transitions between on-ground and off-ground

Temperature was included in the best-fit models but did not have a significant influence on the number of transitions between on-ground and off the ground for Red-capped and Karoo Larks. Null models were selected as the best-fit model for Large-billed and Spike-heeled Larks. However, when comparing the number of transitions between the ground and off the ground for all temperatures among the lark species, Spike-heeled Larks had significantly more transitions than all the other species ($p < 0.05$; Figure 10).

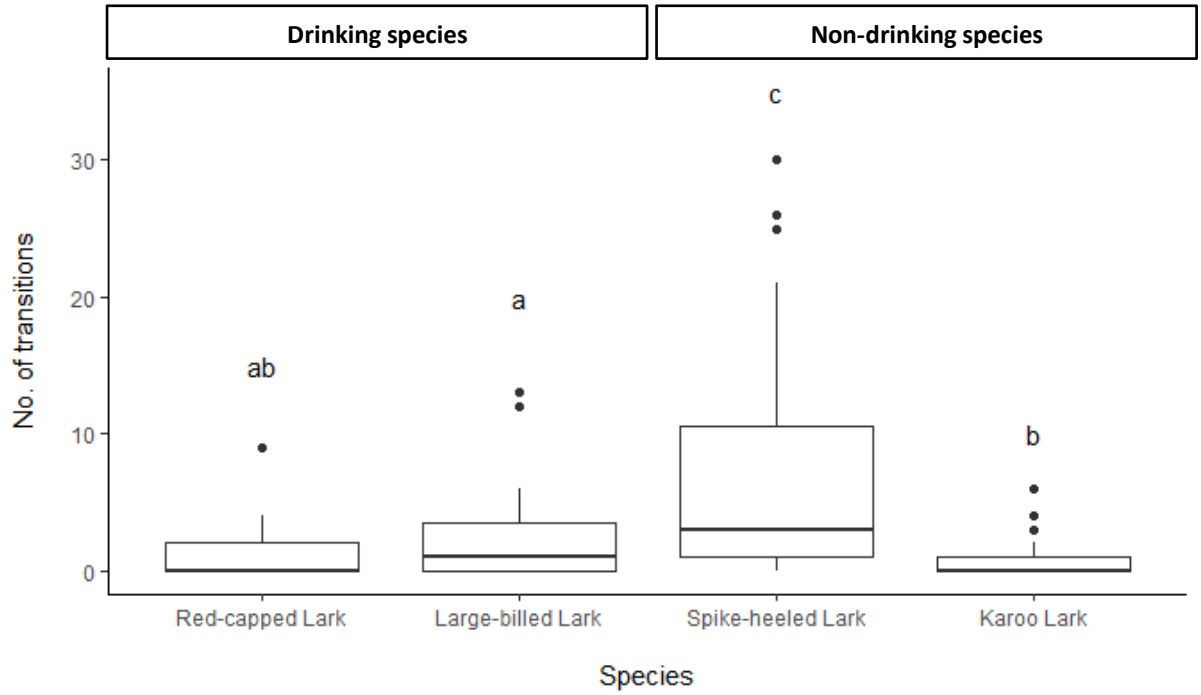

Figure 10 Boxplot comparing the number of transitions between on-ground and off-ground microsites for all temperatures for Red-capped (n = 15), Large-billed (n = 26), Spike-heeled (n = 80) and Karoo Larks (n = 76). Different letters indicate significant differences between species (pairwise Wilcoxon rank sum test; $p < 0.05$).

iv. Peck rates

Larks were observed foraging exclusively on the ground, and as consequence only ground-based microsites were included in analyses of peck rates. The peck rates of all lark species, except Red-capped Larks, were significantly higher in sunny versus shaded microsites on the ground (all $p < 0.05$; Figure 11 and Appendix G). Only one lark species, the Spike-heeled Lark, was ever observed to pant and attempt to forage simultaneously. For this species, peck rates did not significantly differ depending on whether birds were panting or not ($V = 7$, p-value = 0.30).

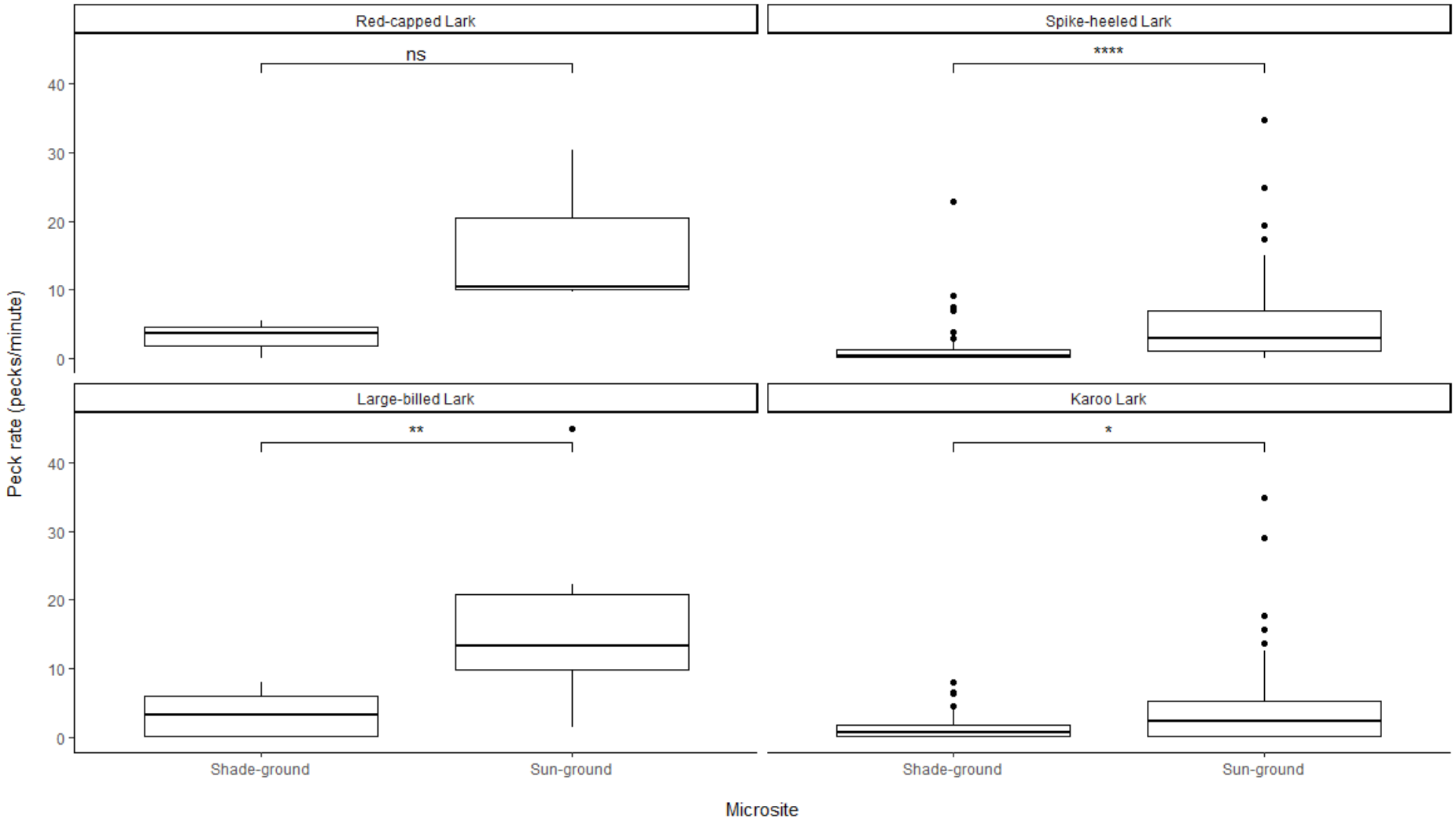

Figure 11 Boxplot showing the peck rate (no. of pecks per minute) in shaded compared to sunny microsites for Red-capped Lark (top left), Spike-heeled lark (top right), Large-billed Lark (bottom left) and Karoo Lark (bottom right) each of the lark species. Asterisk (*) indicates significance (paired Wilcoxon signed rank test; $p < 0.05$).

Discussion

My hypothesis had limited support from scan sample data, which suggested that foraging was more suppressed in larger larks than smaller larks (although this relationship was non-significant). However, in line with my prediction, I found that among the four species of lark (which was supported by scan sample data from other passerines), drinking dependency (drinking surface water, versus water obtained from diet and metabolism) seemed to be more important than body mass in influencing thermoregulatory behaviour and potentially the associated trade-offs between foraging and thermoregulation. The results from scan samples indicated that non-drinking larks seek shade at cooler temperatures, increase heat dissipation significantly with increasing temperature and begin heat dissipating at higher temperatures than drinking larks. Furthermore, focal observation data suggests that the non-drinking larks are more reliant on shuttling thermoregulation (higher rates of transitions from sun to shade and back again) than drinking larks.

The greater reliance on non-evaporative avenues of thermoregulation may make non-drinking larks vulnerable to energetic shortfalls due to thermoregulatory behaviour (such as shade seeking) and thus lower foraging time than drinking larks (Sinervo et al. 2010; du Plessis et al. 2012; Cunningham et al. 2015; Edwards et al. 2015). Focal observation data from this study found that foraging intensity was significantly lower in the shade than in the sun for all lark species, except for Red-capped Lark, which may suggest that shaded microsites offer sub-optimal foraging opportunities (Smit et al. 2013; van de Ven et al. 2019). Without measuring foraging intake directly, it is hard to establish whether higher foraging intensity in sunny microsites than shaded microsites does in fact translate into sunny microsites have higher foraging quality than shaded. Evidence from the scan sample data that drinking larks may be able to remain in the sun as temperatures increase may also validate the idea that non-drinking larks are more vulnerable dehydration and energetic shortfalls. However, there is also evidence from scan sample data to suggest that non-drinking larks might not have a greater susceptibility to these trade-offs. For example, body mass was found to be a better correlate of for_{50} than drinking dependency in scan samples (although this result was non-significant and included only four data points).

Previous studies have found that body mass is an important factor in the suppression of activity (e.g. foraging), with activity being more suppressed in larger species compared to smaller species at high temperatures (Smit et al. 2016; Pattinson et al. 2019). These studies compared species across several taxa and with very different ecologies. For example, Smit et al. (2016) included species such as Spike-heeled Larks and Lilac-breasted Rollers *Coracias caudatus*, which have vastly different foraging strategies. Evidence from the scan samples suggest that this trend may still be present even when species share the same foraging ecology, since foraging (for_{50}) was more suppressed in larger larks than smaller larks. The potential body mass effect observed in the scan samples may be explained by larger birds having a greater evaporative cooling costs than smaller birds and therefore foregoing foraging in order to conserve water (Riddell et al. 2019). Alternatively, larger birds may have a greater capacity to store resources, such as water and energy, than smaller birds (Wolf & Walsberg 1996). As a result, these birds may be able to cease foraging at lower temperatures in order to maximise energetic benefits, while minimising negative impacts on their water balance. For example, in my study, Large-billed Larks were observed to have the highest median peck rate of all the lark species, while restricting foraging to cooler average air temperatures than the other larks. Similarly, when Hoopoe Larks *Alaemon alaudipes* were supplemented with food and water in the Arabian Desert, they reduced their time spent forging and increased thermoregulation (Tieleman & Williams 2002).

Evidence from focal observation data indicated that only non-drinking larks showed a significant decline in foraging with air temperature. Based on the focal observation data, this pattern would suggest a drinking rather than a potential body mass effect (as the data may suggest in the scan sample data). This discordance between the scan sample and focal observation data may be as a result of the smaller sample size obtained in the focal observations or that these data provided important additional detail that was not captured by the scan sample data. However, the drinking effect observed in the focal observation data may reflect the fact that water budgets of drinking species are less likely to be constrained by thermoregulatory costs than those of non-drinking species, being constrained rather by the distance to available surface water (Fisher et al. 1972; Abdu et al. 2018). This indicates that non-drinking species may face more severe trade-offs between foraging and thermoregulation than drinking species and suppress foraging accordingly.

My scan sample results emphasise the importance of drinking dependency and its influence on species' methods for coping with trade-offs between foraging and thermoregulation. Scan sample data revealed that drinking had lower HD_{50} than $shade_{50}$ values, suggesting that drinking larks are able to invest more water in evaporative cooling than non-drinking species when regulating their body temperature (Smit et al. 2016; Czenze et al. 2020). By contrast, non-drinking species obtain the majority of their water through foraging and may lose more water through evaporative cooling during activity than they can easily recoup from their food (Tieleman & Williams 2002; Tieleman et al. 2003; Smit & Mckechnie 2015). Non-drinking species had higher HD_{50} than $shade_{50}$ values, suggesting that these species preferentially utilise passive heat loss (e.g. shade-seeking and shuttling thermoregulation) in order to conserve water through delaying the onset heat dissipation and thus minimising water-costly evaporative cooling (Smit et al. 2016). Similarly, non-drinking lark species had higher HD_{50} values than the two drinking species in scan samples, potentially in order to reduce water expenditure, and a result consistent with the findings of other studies (Smit et al. 2016; Pattinson et al. 2019). This was corroborated by the focal observation data, where non-drinking larks transitioned between sunlit and shaded microsites significantly more than the drinking larks. Therefore, non-drinking species are expected to have a severe trade-off between foraging and thermoregulation; they need to obtain water to avoid dehydration but obtain the majority of water through their diet - requiring them to be active at high temperatures (Dawson 1982; Smit & Mckechnie 2015; van de Ven et al. 2019).

My data suggest that non-drinking lark species in this study may indeed face more severe trade-offs between foraging and thermoregulation than drinking lark species. For example, in scan samples, heat dissipation behaviour increased for all larks at high air temperatures, but the increase was only statistically significant for non-drinking species. Therefore, these birds appear to reduce their thermoregulatory water demands (such as evaporative cooling) through shade-seeking during the hottest periods of the day (Wolf et al. 1996; Riddell et al. 2019). In this study, birds could reduce the black bulb temperatures to which they were exposed by as much as 8.16 °C through moving from the sun into the shade. Although the difference between temperatures in the sun and shade is modest compared to other studies, which have found differences in black bulb temperatures of as much as 20 °C (Carroll et al.

2015), these cooler microsites can reduce rates of heat gain, and/or promote passive heat loss, rather than evaporative cooling, and as a result are a vital method of conserving water (Dawson 1982; Wolf et al. 1996; Wolf 2000; Martin et al. 2015). For example, Hoopoe Larks (a non-drinking species) in the Arabian Desert use lizard burrows during the heat of the day and consequently are able to accrue water savings of up to 81% compared to a bird that remained above ground in the shade (Tieleman & Williams 1999; Tieleman et al. 2003). Therefore, I would anticipate that shade seeking would similarly facilitate water savings for non-drinking species in this study, and indeed Spike-heeled Larks were often observed seeking shade in Aardvark *Orycteropus afer* burrows (pers. obs.). My findings are consistent with the hypothesis that shade-seeking is water-saving behaviour, since both non-drinking larks moved into shade at lower temperatures and significantly more often with increasing temperatures than the drinking larks in scan samples. Moreover, when considering only lark species from this study, drinking species had higher $shade_{50}$ values than non-drinking species. However, when considering all passerine species observed in this study, no differences were observed in $shade_{50}$ between drinking and non-drinking species. The other passerine species observed in this study do not forage on the ground to the same extent as the larks, which may suggest that foraging niche is an important determinant of thermoregulatory behaviour (Louw 2011).

Shade-seeking may not always offer respite from high operative temperatures on the ground. For example, I found that operative temperatures in the shade above air temperatures of 31 °C on the gravel plains were hotter than the temperature on top of a bush approximately 60 cm off the ground. When surface temperatures become too hot, Spike-heeled Larks in the Namib Desert have been observed to suspend activity and seek elevation above ground on bushes and shrubs (Willoughby 1971). In this study, Large-billed Larks were observed to seek off-ground perches more often at high temperatures. This could be explained by the fact that 88% of all the scan samples of Large-billed Larks (n = 42) in this study were on the gravel plains.

Both Red-capped and Large-billed Larks were almost exclusively observed on the gravel plains regions of the park. However, given the results from the black bulbs suggests that the gravel plains are a more thermally challenging environment than the sandy regions in the north and

east of the park, it is unclear why these two species were recorded more often on gravel. This would suggest that another factor other than temperature may play a role in determining their habitat use within the Tankwa Karoo. Data from my focal observations show that foraging behaviour was present in almost every observation for both species on gravel. du Plessis et al. (2012) point out that foraging activity is not driven by heat balance alone but may also be caused by energetic and other requirements. Moreover, if the risk of heat stress and dehydration is outweighed by the energetic costs of not foraging, then these species may continue to forage (du Plessis et al. 2012). Both drinking larks can efficiently replace water lost through evaporative cooling and avoid dehydration by drinking, and as consequence their foraging patterns will rather be driven by energetic costs and requirements. Drinking species may therefore be less prone to trade-offs between thermoregulation and foraging than non-drinking species, as a result of their ability replace to lost water (Czenze et al. 2020). However, due to their reliance on evaporative cooling, drinking species may be more vulnerable to climate change, since the Tankwa Karoo has been observed to be undergoing a drying trend over the last 20 years (van Wilgen et al. 2016).

Because of this reliance on evaporative cooling for thermoregulation, drinking species are expected remain in close proximity to free-standing surface water during the heat of the day in order to replenish expended water (Abdu et al. 2018). A potential movement away from my transects and towards water sources as temperatures increase, may explain the considerably smaller sample size obtained for drinking species in this study, since birds observed within 500 m of the water source were excluded. My observations may thus have been biased in favour of the non-drinking species rather than drinking species. For example, I noted an additional seven Red-capped Lark observations within the 500 m buffer zone, given the small sample size, the inclusion of these observations within my dataset would have increased the sample size by a third.

Comparison of the two sampling techniques

Both scan samples and focal observations are widely used in behavioural studies on birds (du Plessis et al. 2012; Cunningham et al. 2015; Edwards et al. 2015; Martin et al. 2015; Smit et al. 2016; Pattinson & Smit 2017; Pattinson et al. 2019; van de Ven et al. 2019). As I used both methods concurrently to obtain behavioural data on the same focal individuals, this study presents the opportunity to compare the efficacy and accuracy of these two methods. Although I attempted to use both methods on all focal species encountered, individuals (after obtaining scan sample data) would sometimes become startled when detecting the vehicle/observer and subsequently move off. Therefore, I was able to generate a larger sample size for scan samples (n = 286) than focal observations (n = 198). Scan samples are advantageous as they are efficient in terms of time and as a consequence can permit large sample sizes to be collected (Paolisso & Hames 2010). Scan samples are desirable when the focal individual is difficult to observe, and as a consequence, difficult to distinguish behaviours for extended periods of time (e.g. when the bird is in dense bushes; Mann 1999). However, focal observations may provide more detailed behavioural data (Altmann 1974). Using the focal method, I was able to acquire time budget, transition data (between the sun and shade; on- and off-ground) and foraging intensity data, which would not have been possible to collect using scan samples alone. The strengths of focal observations are that they provide continuous data on behaviours over time (Mann 1999). In this study, results obtained from scan sample data always corresponded to the data from focal observations, but the opposite was not true. For example, if a significant result was obtained for focal observations the corresponding scan sample was significant as well. My results are comparable to studies on primates in which scan samples performed relatively well compared to focal observations (Damerose & Hopkins 2002; Gilby et al. 2010). However, there were a number of instances when the results from scan samples were statistically significant and focal observation data were not. This is probably as a result of the reduced sample size in the focal observations, and the discrepancies are discussed in further detail below. Consequently, although scan samples provide data at a lower resolution, the ease, efficiency and sheer volume of data collected through this method suggest it could be preferable in behavioural studies, depending on the research questions.

Caveats and limitations

The foremost limitation experienced in this study was sample size, particularly within focal observations and within drinking species of lark. The limited sample size for focal observations makes it difficult to fully compare the two sampling techniques. For example, scan samples indicated that heat dissipation occurred at lower temperatures for drinking species compared with non-drinking species, however, focal observations indicated there was only a significant effect for Spike-heeled Larks. Similar discrepancies were observed in shade-seeking and foraging. Consequently, it is difficult to draw conclusions based on the conflicting results obtained by the different sampling methods. Furthermore, the drinking effect observed in all behaviours (both in scan samples and focal observation) may be an effect of the larger sample sizes obtained for non-drinking larks compared to drinking larks rather than a genuine difference observed between species with different drinking ecology.

Another important sample size limitation is that I only made comparisons between four species of lark. Previous behavioural studies on birds with similar objectives to this study, collected data from at least 38 species or more (Smit et al. 2016; Pattinson et al. 2019). As a result, no broad conclusions could be made about mass and drinking behaviour due to the small sample size of lark species that were compared in this study. Therefore, the results from this study should be interpreted with caution. It would have been preferable to obtain data from all eight species of lark that have been recorded in the Tankwa Karoo National Park, which would have doubled my sample size. The inclusion of Black-eared Sparrowlarks *Eremopterix australis* and Karoo Long-billed Larks *Certhilauda subcoronata* in this study would also have increased the variation in body mass, with Black-eared Sparrowlarks (14 g; Lloyd 2005) being considerably smaller than the lightest lark (Red-capped Lark; 24 g) included in this study. However, these species were not recorded in sufficient numbers to include in the study, with sparrowlarks not being recorded at all, likely due to ongoing drought conditions in the Tankwa Karoo. Due to their similar ecologies and diversity in arid environments, larks remain an ideal model system in which to test these hypotheses (Dean 1995; Williams & Tieleman 2001). Future studies with larger samples of lark species could investigate the interactions between body mass and drinking to better understand the results obtained in this study.

Conservation Implications

My study revealed that drinking birds are able to remain in the sun and potentially continue to forage longer than non-drinkers. As a consequence, drinking species may be less vulnerable to missed opportunity costs than non-drinking species as temperatures rise. However, my data also highlighted the dependence of drinking species on free-standing water for thermoregulation, as access to water may be a crucial factor permitting these species to persist within arid environments (Abdu et al. 2018). Data from the last 20 years, suggests that the Tankwa Karoo National Park is becoming increasingly dry (van Wilgen et al. 2016). Current climate change predictions suggest that there will be declines in precipitation over the southwestern parts of South Africa (Niang et al. 2014). Declines in precipitation, in the Mojave Desert of North America have been identified as an important driver in the collapse of the avifaunal community there over the past century (Iknayan & Beissinger 2018). Drinking dependency may influence species' vulnerability to declines in precipitation. Therefore, non-drinking species may be vulnerable to foraging-thermoregulation trade-offs with increasing aridity, while drinking species may become vulnerable to dehydration, impaired thermoregulation and/or hyperthermia in the future due to their dependence on surface water to predictably replenish water lost through thermoregulation (Czenze et al. 2020). Furthermore, this study emphasises the important role of artificial water sources in Tankwa Karoo National Park, the presence of which may reduce water stress and aid in the continued persistence of drinking species in the region.

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Appendices

Appendix A LM comparing air temperature and black bulb temperatures in all three microsites and both substrates.

Microsites	Substrate	df	Estimate	Std. Error	t value	p-value
Shade-ground	Gravel	4388	1.07410	0.008075	133.0	<0.001
Sun-bush	Gravel	4388	0.898539	0.008201	109.57	<0.001
Sun-ground	Gravel	4388	0.92670	0.01196	77.50	<0.001
Shade-ground	Sandy	4372	1.022454	0.005908	173.07	<0.001
Sun-bush	Sandy	4372	0.908873	0.008121	111.92	<0.001
Sun-ground	Sandy	4381	0.88927	0.01178	75.52	<0.001

Appendix B ANOVA and ghlt post hoc comparing black bulb temperatures between and within microsites and substrates.

Substrate and microsite comparisons	Estimate	Std. Error	t value	p-value
Gravel sun-bush – Gravel shade-ground	0.4056	0.1423	2.850	<0.01
Gravel sun-ground – Gravel shade-ground	6.4869	0.1423	45.582	<0.001
Sandy shade-ground – Gravel shade-ground*	-3.0362	0.1423	-21.335	<0.001
Sandy sun-bush – Gravel shade-ground	-0.7751	0.1423	-5.447	<0.001
Sandy sun-ground – Gravel shade-ground	3.5137	0.1439	24.410	<0.001
Gravel sun-ground – Gravel sun-bush	6.0814	0.1423	42.733	<0.001
Sandy shade-ground – Gravel sun-bush	-3.4417	0.1423	-24.814	<0.001
Sandy sun-bush – Gravel sun-bush*	-1.1807	0.1423	-8.296	<0.001
Sandy sun-ground – Gravel sun-bush	3.1082	0.1423	21.593	<0.001
Sandy shade-ground – Gravel sun-ground	-9.5231	0.1423	-66.917	<0.001
Sandy sun-bush - Gravel sun-ground	-7.2621	0.1423	-51.029	<0.001
Sandy sun-ground - Gravel sun-ground*	-2.9732	0.1439	-20.656	<0.001
Sandy sun-bush – Sandy shade-ground	2.2610	0.1423	15.888	<0.001
Sandy sun-ground - Sandy shade-ground	6.54499	0.1439	45.503	<0.001
Sandy sun-ground - Sandy sun-bush	4.2888	0.1439	29.795	<0.001

* Comparisons of substrates

Appendix C Interaction between air temperature and substrate for each microsite in linear models.

Air temperature: substrate	df	Estimate	Std. Error	t value	p-value
Shade-ground	8760	-0.051736	0.010010	-5.169	<0.001
Sun-ground	8569	-0.03743	0.01680	-2.228	<0.05
Sun-bush	8760	0.010334	0.011541	0.895	0.371

Appendix D Models that did not converge in the time budget analysis

Species	Behaviour	No. of models that did not converge
Karoo Lark	Foraging	1
Red-capped Lark	Shade-seeking	5
Red-capped Lark	Height seeking	2

Appendix E Transitions between sun and shade error distribution and variance for each species.

Species	Error distribution	Variance
Red-capped Lark	Poisson	λ
Spike-heeled Lark	Negative binomial "type 1"	φμ
Karoo Lark	Negative binomial "type 1"	φμ
Large-billed Lark	Poisson	λ

λ – is variance in dependent variables that is not explained by differences in levels of the independent variable
φμ -. is a model family standard in the package glmmADMB and this variance structure was the best fit to my data

Appendix F Transitions between ground and off ground error distribution and variance for each species

Species	Error distribution	Variance
Red-capped Lark	Poisson	λ
Spike-heeled Lark	Negative binomial 'type 1"	φμ
Karoo Lark	Negative binomial "type 1" (zero-inflated)	φμ
Large-billed Lark	Negative binomial 'type 1"	φμ

λ – is variance in dependent variables that is not explained by differences in levels of the independent variable
φμ -. is a model family standard in the package glmmADMB and this variance structure was the best fit to my data

Appendix G Wilcoxon signed rank tests comparing peck rates in sunny versus shaded microsites for: Red-capped Lark, Spike-heeled Lark, Karoo Lark and Large-billed Lark.

Species	V	p-value
Red-capped Lark	0	>0.05
Spike-heeled Lark	244	<0.001
Karoo Lark	500	<0.05
Large-billed Lark	2	<0.05